Courtesy M.J. Mac, NBS

Hawaii

by
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Overview

Of the thousands of islands in the world's oceans, none has captured the fancy and dreams of adventure more than those in the central and south Pacific. Even among those magical islands, however, the Hawaiian Archipelago stands out. Mark Twain remarked in *Roughing It*, "They are the loveliest fleet of islands that lies anchored in any ocean."

The Hawaiian Islands are geographically diverse. Stretching over some 2,200 km (364 mi) of ocean, they vary in size from hectares to thousands of square kilometers and in elevation from sun-drenched atolls less than 6 m (20 ft) above sea level up to snow-capped peaks 4,270 m (14,000 ft) high. Rainfall ranges from less than 50 cm (20 in) to more than 1,140 cm (450 in) per year. This diversity of environments and the islands' extreme isolation (more than 4,000 km [2,490 mi] to the nearest continent) have resulted in a spectacular variety of species. The Hawaiian Islands are a true showcase of evolution that has resulted in degrees of endemism (species restricted to a particular area) unmatched anywhere else in the world. Studies show that on Hawaii 46% of mosses, 70% of ferns, 91% of flowering plants, 91% of gymnosperms, 99% of terrestrial mollusks and terrestrial arthropods, 100% of land mammals, and 81% of birds are endemic at the subspecies level (Gagné 1988).

Unfortunately, loss of species in the islands has been staggering, and what remains often occupies but a fraction of its historical range. Seventy percent of the extinctions known to have occurred in the United States took place in Hawaii. The islands have lost more than 50% of their birds (Scott et al. 1986; Scott et al. 1988; Olson and James 1991; Pyle, this section; Jacobi and Atkinson, this section); perhaps 50% of their plants, 90% of their native land snails, and an unknown percentage of their terrestrial insects. Flora and fauna that evolved over millions of years have been devastated in less than 2,000 years since the arrival of humans. But despite huge losses, what remains is spectacular.

Today's unique assemblage of species is rapidly being lost. Twenty-five percent of the U.S. endangered taxa occur in the islands. The reasons for their endangerment are many, but loss of habitat and introduction of non-native species are prominent factors. Both are the result of a steadily increasing human population and the more than 4 million tourists that visit the islands annually. Few visitors realize that the lush lowland vegetation and colorful flowers they marvel at are not native to the islands, but

Hawaii Biological Survey

by
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In 1992 the Hawaii State Legislature established a biological survey at Bishop Museum, Hawaii's Museum of Natural and Cultural History. The survey conducts an ongoing natural history inventory of the archipelago and locates, identifies, evaluates, and maintains the reference collections of all native and non-native species of flora and fauna within the state. The survey works in cooperation with other agencies, including the Hawaii Heritage Program, various state agencies, and the National Biological Service.

More than 14,000 terrestrial, 300 freshwater, and 4,000 marine species inhabit Hawaii (Table 1). Bishop Museum maintains the world's largest biological collections for Hawaii (ca. 4,000,000 specimens; Table 2). Through the Hawaii Biological Survey program, and in cooperation with many partner organizations, the museum is organizing information from these collections and associated literature into comprehensive computerized data bases and conducting field surveys to document distributions of these organisms. The resulting information base has many applications in conservation, agriculture, forestry, public health, fisheries, and land management.

Table 1. Terrestrial and freshwater plant and animal species in Hawaii. In addition, another 4,000 marine organisms inhabit Hawaiian waters. Species at risk include those on the federal lists of endangered, threatened, and candidate species (not including marine).

Taxon	Species (no.)	Endemic (%)	Species at risk
Lower plants	>1,800	Few	0
Higher plants	2,143	44	359
Nematodes	>147	Few	0
Mollusks	1,100	95	60
Insects and mites	>8,800	>60	340
Fish	>25	24	1
Amphibians	4	0	0
Reptiles	13	0	0
Birds	131	43	35
Mammals	19	5	0
Total	>14,182		795

In 1992 and 1993, the Hawaii Biological Survey:

- published a summary list of the more than 8,600 species of Hawaiian insects and related arthropods;
- produced a catalog of Hawaiian land snails, including nearly 1,000 species;
- continued progress on the book series *Reef and Shore Fauna of Hawaii*, with another volume nearing completion; and
- began a collaborative project with the Smithsonian Institution and local agencies to create a data base of specimens of Hawaiian plants. Other plant projects in progress include a manual of cultivated plants in Hawaii (2,500 species treated in detail, with an additional 10,000 species evaluated); a manual of marine algae; and an updated, electronic bibliography of Hawaiian plants.

A five-stage process was developed to implement the biological survey. For each major group of plants and animals, the process involves developing a computerized literature data base; preparing summary lists of species names (checklists) based on the literature, collections, and consultation with experts; creating a data base of specimen information in our collections; creating data bases of information from other collections and other sources or establishing computer linkage to this information; and filling gaps and updating information through field surveys.

Courtesy D. Polhemus, Bishop Museum

Megalagrion pacificum, a damselfly in a genus endemic to the Hawaiian Islands.

Table 2. The comprehensive collections of Bishop Museum are a core resource for the Hawaii Biological Survey. This chart indicates the relative sizes of the Hawaiian collections, plus related materials from the Pacific region and elsewhere that provide the context for understanding the Hawaiian biota.

Group	Hawaiian collections	Total collections	%
Plants (including algae, etc.)	175,000	500,000	35
Marine invertebrates	250,000	500,000	50
Mollusks	3,000,000	6,000,000	50
Insects and mites	500,000	13,000,000	4
Fish	15,000	130,000	12
Terrestrial vertebrates	20,000	85,000	24
Library		100,000	
Archives		1,100,000	

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are instead a diverse collection of alien invaders that pose the biggest threat to the integrity of Hawaii's native ecosystems.

The alien species that have had the greatest impact on Hawaii's fragile flora and fauna, however, are the ungulates (e.g., pigs, goats, sheep, and cattle), which have devastated the native plants that evolved in the absence of grazers and browsers and thus had lost any protective mechanisms they might have had. Pigs have been particularly damaging, rooting through the understory, devastating large tracts of land, and creating a seedbed for alien plants and severe erosion, especially on the steep slopes of older islands. Elimination of alien species and prevention of invasion by new non-native species are the first conservation priority in Hawaii (Stone and Scott 1985; Stone et al. 1992).

Status and trends of the amazingly diverse insects of Hawaii are described by Howarth et al. (this section). The case for using species of picture wing flies as monitors for change and evolution is made by Foote and Carson (this section), while the dramatic recovery of a plant, the Haleakala silversword (Loope and Medeiros, this section), gives hope that other species can respond to recovery efforts. There are lessons to be learned not only from our failures, but also from successes such as the silversword.

Interest in the plants and animals of Hawaii has rekindled in the last 20 years. Private, state, and federal biologists have sought to document the occurrence and abundance of species and have mounted an impressive attempt to save the remaining characters in this hotbed of evolution (*see* Vol. 38 of *BioScience* and Culliney 1988 for a review). To gain more information about Hawaii's resources, the state legislature formed the Hawaii Biological Survey in 1992, whose mission and scope are described in this section (Allison et al.).

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Haleakala Silversword

by

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The Haleakala silversword (*Argyroxiphium sandwicense* ssp. *macrocephalum*) was near extinction in the 1920's because of human vandalism and browsing by goats and cattle. The plant has increased under protection and deserves attention as the most dramatic conservation success story of the Hawaiian Islands.

The silversword is a distinctive, globe-shaped rosette plant with rigid (sword-like), succulent leaves densely covered by silver hairs. When a plant flowers at the end of its life, it produces a spectacular flowering stalk 0.5-2.0 m (1.6-6.4 ft) tall, typically with hundreds of maroon sunflowerlike flower heads. This plant receives more attention from visitors to Haleakala National Park than any other plant or animal because of its striking appearance and restricted distribution.

The Haleakala silversword is endemic to a 1,000-ha (2,471-acre) area at 2,100- to 3,000-m (6,890- to 9,843-ft) elevation in the crater and outer slopes of Haleakala Volcano, within Haleakala National Park, Maui, Hawaii. It is the most famous member of the endemic Hawaiian silversword alliance, perhaps the premier example of evolutionary adaptive radiation in plants. This morphologically diverse group comprises 28 species of herbs, vines, shrubs, trees, and rosette plants in three genera that evolved in the Hawaiian Islands from a North American tarweed (Asteraceae: Madiinae) ancestor (Robichaux et al. 1990; Baldwin et al. 1991). The monocarpic (flowers only once, at the end of its lifetime) silversword matures from seed to its final flowering stage in about 15-50 years. The plant remains a compact rosette until it sends up an erect, central flowering stalk, sets seed, and dies.

In 1992 this taxon was given threatened status by the U.S. Fish and Wildlife Service because of its extremely limited range and precarious life cycle. The other subspecies of *A. sandwicense* (ssp. *sandwicense*), endemic to Mauna Kea on the island of Hawaii, is federally listed as endangered, with fewer than 100 naturally occurring individuals.

Population Trends

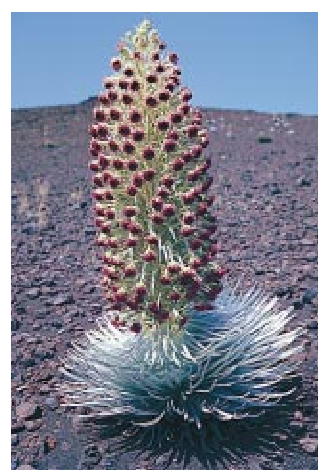
The strikingly beautiful Haleakala silversword has always aroused the curiosity of human visitors to Haleakala Volcano. In pre-park days, plants were often removed by travelers to Haleakala Volcano as proof that the party had reached the summit, a practice that eventually seriously affected the silversword population. Browsing by feral goats and domestic cattle was also a significant factor in the silversword decline, but it was not a species preferred by these animals. By the 1920's, silversword numbers were so depleted that the Maui Chamber of Commerce sent a petition to Washington, DC, requesting that a serious effort be made to save the species (Loope and Crivellone 1986).

The first reliable quantitative information on silversword numbers is from the summer of 1935. In that year, Ranger S.H. Lamb tallied 1,470 plants (88 of which were flowering) on a single cinder cone (Ka Moa o Pele) within Haleakala Crater (Lamb 1935). Because about 217 plants were flowering within the crater at that time (Lamb 1935), a reasonable estimate of the total population is about 4,000 individuals.

Because silversword plants occur on otherwise barren cinder, fairly accurate counts are possible. Two studies since 1935 illustrate the trend of the silversword population over about 60 years of protection. Methods are described in the original reports (Kobayashi 1973, 1993; Loope and Crivellone 1986).

On Ka Moa o Pele, a single cinder cone where the largest number of plants were in 1935, the silversword population had increased from 1,470 to 6,528 plants as of 1991 (Fig. 1).

Elsewhere in Haleakala Crater, the silversword has increased in numbers and extent, large local populations having developed in areas where few plants occurred in 1935. A census of the entire silversword population has been attempted four times since 1971, with the following results: 1971: 43,262 (Kobayashi 1973); 1979-80: 35,000 (Kobayashi 1993); 1982: 47,640 (Loope and Crivellone 1986); and 1991:



Courtesy A.C. Medeiros, NBS

Haleakala silversword (*Argyroxiphium sandwicense* ssp. *macrocephalum*).

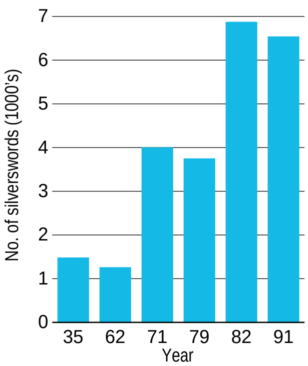


Fig. 1. Number of silversword plants counted by investigators on a single cinder cone, Ka Moa o Pele, within Haleakala Crater (Loope and Crivellone 1986; Kobayashi 1993).

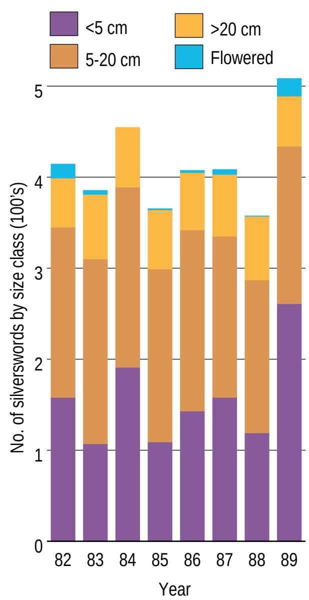


Fig. 2. Number by diameter classes of Haleakala silversword in fixed monitoring plots, 1982-89. Summary of data from eleven 5 m x 20 m (16.4 x 65.6 ft) plots in representative sites in Haleakala Crater (Loope and Medeiros 1994).

64,800 (Kobayashi 1993). The current population of Haleakala silversword is about 16 times larger than the estimated population in 1935.

Annual trends in 11 fixed plots, 5 m x 20 m (16.4 x 65.5 ft), from 1982 through 1989, suggest occurrence of substantial annual fluctuations in the recruitment and survival of seedlings (Loope and Crivellone 1986; Loope and Medeiros 1994; Fig. 2).

Data on Silversword Flowering

The Haleakala silversword flowers from June to September, with annual numbers of flowering plants varying dramatically from year to year. Reliable counts of flowering plants were made in 1935 (217 flowered) and in 1941 (815 flowered; Loope and Crivellone 1986). Numbers recorded in recent years have ranged from zero in 1970 to 6,632 in 1991. The environmental stimulus for flowering or nonflowering of silversword within a given annual flowering season is still unknown. An apparent relationship of the 1991 mass flowering event to stratospheric alteration by the eruption of Pinatubo Volcano in the Philippines is intriguing.

Threats

As a result of management within Haleakala National Park, the most serious former threats to the Haleakala silversword have been virtually eliminated: human vandalism and browsing by goats and cattle. To date, no introduced plant species competes significantly with silversword. Cooperative interagency efforts are being made to exclude the non-native mullein (*Verbascum thapsus*) and fountain grass (*Pennisetum setaceum*) from becoming established on Maui; since these plants occupy similar habitat on other Hawaiian Islands, they might compete with silverswords.

The greatest threat to the silversword appears to be potential loss of endemic pollinators because of the invasion of silversword habitat by the Argentine ant (*Iridomyrmex humilis*). This ant species occupies two disjunct areas between 2,070 m (6,792 ft) and 2,850 m (9,351 ft) elevation in Haleakala National Park, with a total area of 175 ha (432 acres; Cole et al. 1992). Because queens are unable to fly, the spread of this species is relatively slow. This alien ant species negatively affects the locally endemic arthropod fauna (Cole et al. 1992), including pollinators that evolved in the absence of ant predation. A marked expansion in the ant's range was noted in 1993, especially at higher elevations (Medeiros et al. 1994). Unless this ant species is controlled, it could cause potentially catastrophic effects on locally endemic biota, including the silversword, which is associated with several endemic insect species (Loope and Crivellone 1986) and which requires cross-pollination for successful seed set (Carr et al. 1986). Experimental control efforts are under way.

Trends

Recovery of the Haleakala silversword is one of the most dramatic single-species conservation success stories known. The primary factor contributing to its decline, human vandalism, was effectively addressed by the National Park Service beginning in the 1930's. Over the past 60 years the species has steadily recovered through protection within Haleakala National Park. It is increasing in numbers and expanding its range. Continued protection from human vandalism and feral ungulates, such as goats and cattle, is essential, and potential threats from the Argentine ant and alien plants must be addressed. Given the plant's limited range and precarious life cycle, the long-term prognosis for survival of this species appears remarkably favorable.

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Insects of Hawaii

by
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Insects are the dominant animals in most terrestrial ecosystems, especially on isolated oceanic islands where many larger animals are absent. In Hawaii, many of the original colonizing species evolved into perhaps 10,000 or more new species and adapted to live in the diverse island habitats. In addition to their importance as pollinators of native plants, recyclers of nutrients in ecosystems, and food for native birds and other animals, insects are also excellent subjects for evolutionary research. The isolation and habitat diversity of the Hawaiian Islands make them wonderful natural laboratories for studying ecology and evolution. Many important research projects have featured Hawaiian insects, such as the native *Drosophila* (*see* Foote and Carson, this section) and crickets (Otte 1989).

Because insects are important components of ecosystems, insect surveys can be used to assess the health of native ecosystems, and reserve managers often need to be able to determine the status of insects to properly manage other natural resources. Such assessments, however, are daunting tasks: although about 5,100 native insect species have been described in Hawaii, probably at least as many more remain undescribed or unknown. In addition, about 2,600 insect species have been established through human activities. Many native species are declining from the combined effects of invasive non-native organisms and human alteration of habitats.

Information on the status of Hawaiian insects came from a data base compiled at the Bishop Museum of all published records on the taxonomy, biology, and distribution of Hawaiian arthropods (Nishida 1992). Further information on the status and trends of selected rare species was obtained from label data of preserved specimens, especially those in the research collections at Bishop Museum and University of Hawaii, Honolulu, as well as from personal communications and observations of researchers in the field. Population surveys are in progress to determine the status and trends of a few insect groups such as the damselflies (*Megalagrion*; Polhemus 1993) and cave species.

Insects of Hawaii

Only 16 out of 30 insect orders recognized worldwide are represented in the native fauna. Another 11 orders have become established through human activities (Figs. 1 and 2). The beetles (Coleoptera), flies (Diptera), bees and wasps (Hymenoptera), and moths (Lepidoptera) are the largest groups in the Hawaiian Islands. Most native species are found on the high, main islands, but each of the northwest Hawaiian Islands harbors a few interesting species (Fig. 3). Oahu currently has the most known species, but this stems from collecting bias because most entomologists have lived and worked on Oahu. Maui and Kauai, in particular, should have comparable numbers. Western Maui, for example, was missed in the early insect surveys, and its insect fauna remains poorly known. About 63% of the species occur on only one island, and many have extremely restricted ranges within their island. This limited distribution and lack of information on how many species there are and where they survive have important consequences in planning for their conservation.

Trends

Profound changes are occurring in the Hawaiian insect fauna. Increasing contact with the outside world has broken the isolation that allowed the evolution of native species. The changing composition of the Hawaiian insect

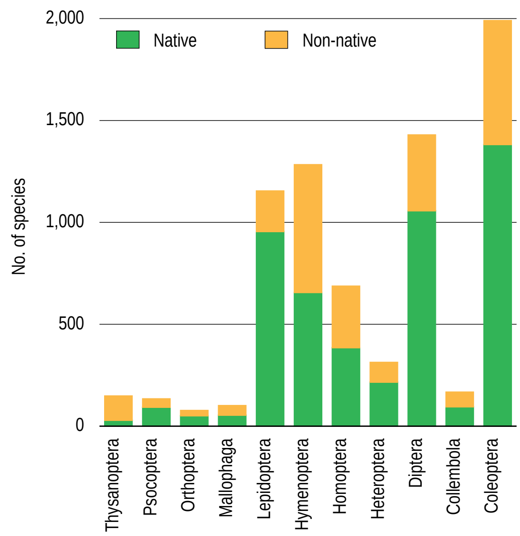

Fig. 1. Comparison of native and non-native insects in the larger orders (i.e., represented by more than 75 species) in Hawaii. Source: Hawaiian Terrestrial Arthropod Database, February 1994.

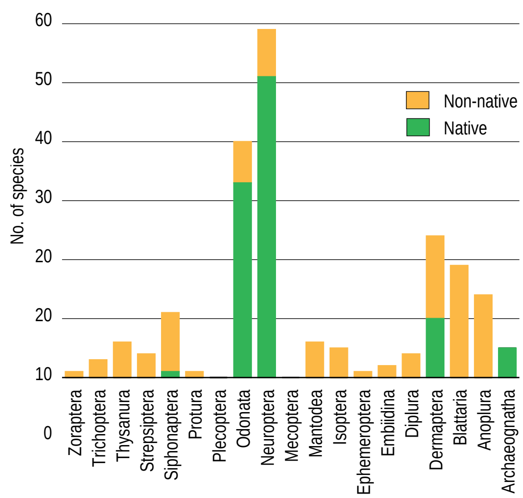

Fig. 2. Comparison of native and non-native insects in the smaller orders (i.e., represented by fewer than 75 species) in Hawaii. Source: Hawaiian Terrestrial Arthropod Database, February 1994.

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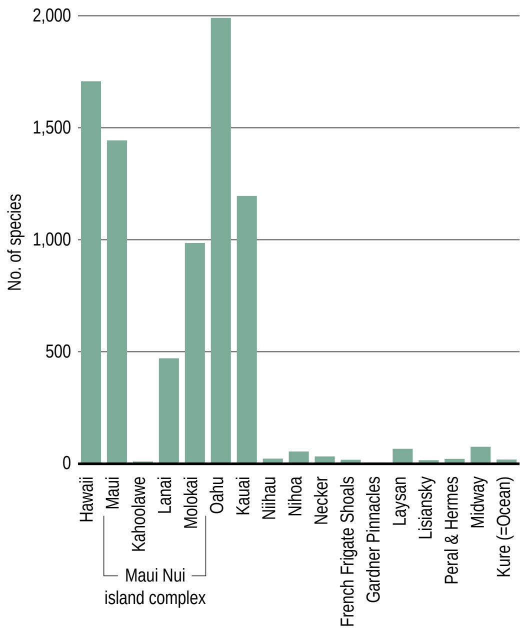


Fig. 3. The island distribution of native insect species.

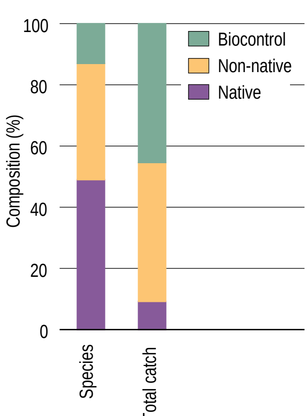


Fig. 4. Species and total catch composition of wasps in the families Braconidae and Ichneumonidae in a high-elevation mesic forest on the Hawaiian island of Kauai. Wasps were sampled from January 1992 to January 1993 by using a Malaise trap.

fauna is readily apparent from the contrast between historical collections and reports (e.g., Perkins 1913; Zimmerman 1948) and more recent records and surveys. This change is particularly obvious in lowland areas where land conversion (Cuddihy and Stone 1990) and the establishment of alien species have eliminated or drastically reduced the abundance and diversity of native arthropods. For example, Asquith and Messing (1993) found that less than 10% of the insect fauna of a lowland agricultural area on Kauai is composed of native species, and, at a low-elevation site on the island of Hawaii, even the arthropod community on the native tree ‘Ohi ‘a lehua (*Metrosideros polymorpha*) is composed primarily of alien species (Gagné 1979).

At higher elevations in more intact vegetative communities, invasive alien arthropods have become dominant in some guilds, such as honey bees as pollinators and millipedes and isopods as detritivores. The effects of predatory species, such as the Argentine ant (*Linepithema humilis*; Cole et al. 1992) and the western yellowjacket (*Vespula pensylvanica*; Gambino et al. 1990), in the decline of some native groups are well documented.

Introduced Parasites

Although the native Hawaiian faunas naturally bear some pressure from parasitoids, with endemic taxa of wasps in the families Ichneumonidae, Bethylidae, Diapriidae, Eucoiliidae, and Eulophidae, and the fly family Pipunculidae, the taxonomic composition and therefore the ecology of parasitism itself have been altered by the addition of alien species. For example, the Hawaiian Islands originally had no native species of braconid wasps, but now harbor 76 species in 42 genera (Nishida 1992). Many of these parasitoids are not confined to disturbed habitats or alien hosts. By using a Malaise trap (a tentlike net left in place to capture flying insects), A. Asquith and M. Kido (USFWS and University of Hawaii, Kauai, unpublished data) recently sampled the parasitic wasp community in a high-elevation native mesic forest on the island of Kauai for a full year. Of the 17 species of Braconidae and Ichneumonidae captured, all but one are parasitoids of moth larvae and pupae, and all but two are known to attack native Hawaiian moths. No known species of native ichneumonid wasp in this forest is extinct, and the endemic taxa still contribute the most to species diversity (Fig. 4). Human activities, however, have essentially doubled the number of species parasitizing native Lepidoptera. Furthermore, parasitoid abundance in this community is dominated by non-native species (Fig. 4), with less than 1 in 10 parasitoids being native to Hawaii. On a numbers of individuals per species basis, the two species introduced for biological control (*Eriborus sinicus* and *Meteorus laphygmae*) are more invasive in this forest than the supposed inadvertently introduced species of parasitoids. Not only have these introductions increased the number of species and individuals parasitizing Hawaii’s native Lepidoptera, but also the new species have searching and immobilizing behaviors to which the native fauna is unaccustomed.

Populations of the native stink bug (Pentatomidae) genera *Coleotichus* and *Oechalia* dramatically decreased after 1962 following the purposeful introductions of a tachinid fly and several scelionid wasps for biological control of the non-native pest, the southern green stink bug (*Nezara viridula*). The koa bug (*Coleotichus blackburniae*) is the largest and most spectacular native Hawaiian true bug and was, until the early 1970’s, common on all the major Hawaiian islands, including within the city of Honolulu, where it could frequently be found on introduced acacia trees. Numerous specimens were deposited in the insect collections of the Bishop Museum and University of Hawaii every decade from 1890 to 1970, but very few specimens have been seen since 1978. Because the koa bug is conspicuous, and its rarity has been publicized (Howarth 1991), its population decline seems real and not an artifact of survey effort.

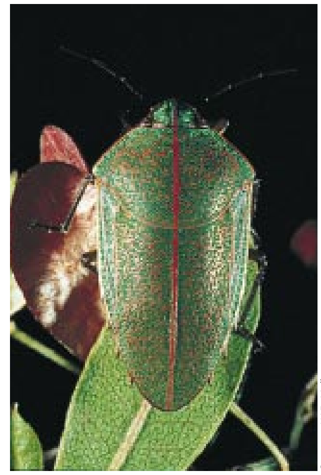
Since the koa bug is gregarious and hundreds of individuals could be collected from a single tree, it was used as an alternate host for rearing introduced parasites before their release. Thus, circumstantial evidence implicates these biological-control introductions in the demise of these native bugs. Recent observations suggest that small populations of the koa bug still survive on most of the major islands, but quantitative status surveys and protection for this insect may need to be initiated to ensure its continued existence.

These examples support the arguments of Gagné and Howarth (1985) and Howarth (1991) that alien parasitoids are the major factor contributing to the decline and extinction of many native insect species. Lepidopteran caterpillars were an important food source for native forest birds and other native organisms; thus, their decline may affect other parts of the forest community. The ability of non-native arthropods to invade intact native communities demonstrates that conservation efforts aimed at habitat preservation, or the selection and management of nature reserves based on plant diversity or endemism, may not provide sufficient protection for some insects and their associated biota because of the continued emphasis on biological control and insufficient quarantine control in Hawaii. The effect of invasive alien arthropods means that we could save the forest and still lose the bugs, but we would eventually lose the forest as well because of the loss of pollinators and other functional groups of insects.

Extinctions

With at least 50% of Hawaii's native birds (Stone 1989) and mollusks (Solem 1990) extinct, it is likely that Hawaii has also lost a significant proportion of its terrestrial arthropod fauna. While 36 arthropod species are recognized as extinct by the U.S. Fish and Wildlife Service, populations of two species, a damselfly (*Megalagrion nesiotes*) and a sphinx moth (*Manduca blackburni*), have recently been rediscovered. The lack of intensive surveys for most of Hawaii's rare arthropods makes their status equivocal and weakens arguments for the allocation of conservation resources for these animals.

One of the few areas in Hawaii where arthropod extinctions are reasonably well documented is on Laysan Island in the northwestern part of the chain. While only 3.8 km^2 (1.5 mi^2) in size, it harbored at one time a native arthropod fauna of at least 77 taxa with at least 14 endemic species (Conant et al. 1984). With intensive surveys during the 1960's and 1980's, we now know that 35% of Laysan's endemic species are extinct. Other evidence of arthropod extinctions comes from those species associated with endangered or extinct plants. In 1917 a new species of *Proterhinus* weevil was collected from the last remaining tree of *Hibiscadelphus giffardianus* on the island of Hawaii. While the tree has been given a reprieve from extinction by propagation of individuals from seed, the weevil, which breeds in dying branches, was doomed with the death of the last wild tree. Many Hawaiian insect groups are similarly extremely host-specific; for example, some species of long-horned beetles (*Plagithmysus*), with 139 known species, and leaf bugs (*Nesiomiris*), with 50 species, occur on rare hosts and face a similar fate.


Courtesy W.P. Mull

The koa bug (*Coleotichus blackburniae*), the largest Hawaiian true bug (three-fourths inch long), was common, but few have been seen since 1978.

Survey Needs

Waiting for confirmations of extinctions or the discoveries of relict populations is ineffective, reactive conservation and will not preserve Hawaii's remaining arthropods. We need to identify species early in their decline or at least before they slide beyond recovery (Howarth and Ramsay 1991). This report is limited to the insects, but other native invertebrates deserve mention, including the spiders and relatives (arachnids), sandhoppers and relatives (crustaceans) (Howarth and Mull 1992; Nishida 1992), and mollusks (Solem 1990; Cowie et al., in press). The worms and smaller invertebrate groups are even less well-known than the arthropods.

The urgency and effectiveness of status surveys are exemplified by one being conducted for Hawaii's damselflies. On the island of Oahu alone, two damselfly species are believed extinct, and three additional taxa are severely reduced from their historical ranges and in danger of extinction. For example, sometime between 1983 and 1985, *Megalagrion nigrohamatum nigrolineatum* disappeared from its usual haunts along streams near Honolulu. Surveys begun in 1990 have found it in only three isolated localities near the headwaters of Oahu streams. This represents a greater than 99% reduction in range in a decade. Most of its former habitat still appears suitable and the reasons for its decline are uncertain, but researchers suspect the decline results from the effects of non-native species, as well as habitat destruction (Polhemus 1993).

Status surveys of additional selected groups of arthropods should be a top priority so that appropriate conservation measures can be planned. Studies on the systematics of Hawaiian biota, including descriptions of new species, are also urgently needed. Whether a population represents a native or non-native species or 1, 10, or 20 closely related species has bearing on effective conservation strategies in reserves (Howarth and Ramsay 1991).

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Drosophila as Monitors of Change in Hawaiian Ecosystems

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Most of the world's named species of plants and animals are insects, which are the dominant component of the biological diversity of most terrestrial and aquatic ecosystems (Hammond 1992). In Hawaii, there are probably more than 10,000 native insect species, whose functions in Hawaiian ecosystems include prey for forest birds, pollinators of native plants, and decomposers associated with the cycling of plant nutrients.

The population trends and distributions for most Hawaiian insects are unknown and cannot possibly be determined for more than a small minority of species. To successfully develop management strategies to monitor and preserve our biological heritage, focal taxa or "indicator species" need to be identified and used to develop the biological information necessary for making management decisions (Quinn and Karr 1993). The data discussed here demonstrate how one well-studied group of Hawaiian insects, the Hawaiian *Drosophila* (Pomace flies), may serve as a focal insect taxon. The species diversity, underlying genetic diversity, and evolutionary history of this group have been described in detail. Their sensitivity to direct and indirect environmental change has also been demonstrated. These attributes make them an ideal model species to monitor and understand changes in patterns of biological diversity associated with human impacts on native ecosystems in Hawaii.

Background

Hawaiian *Drosophila* and, in particular, the large "picture-winged" species within the genus, are unique among living organisms because different levels of biological diversity within a single large, closely related group of species can be characterized by researchers. Polymorphisms (*see* glossary) due to inverted chromosomal segments have been used to assess genetic variation within and between species. The banding patterns of all five major chromosome arms among 106 species of Hawaiian picture-winged *Drosophila* have yielded a 5 million-year-old phylogeny (*see* glossary) that is rooted to species on the island of Kauai (Carson 1992). This work on the evolutionary history of Hawaiian *Drosophila* augments an extensive systematic treatment of the genus (Hardy 1965; Kaneshiro 1976).

More recent genetic surveys have complemented research on chromosome variation. These include the description of nuclear and mitochondrial DNA sequences and extensive fieldwork that describes genetic variation within and among populations and species of Hawaiian *Drosophila* for allozymes (*see* glossary) and quantitative traits (Carson et al. 1981; DeSalle and Hunt 1987). Attention has focused on characters thought to play an important role in speciation, the process underlying the diversification of *Drosophila* in Hawaii.

Molecular and cytological (*see* glossary) research has been paralleled by ecological research on the natural breeding sites of these species on specific Hawaiian plants, such as olapa (Araliaceae) and ohawai (lobelioids). Extensive surveys have determined that Hawaiian *Drosophila* are specialized microbivores (*see* glossary) that complete their life cycle in the decaying tissue of over 40 families of Hawaiian plants (Carson and Kaneshiro 1976). This ecological information is the most detailed for any group of native Hawaiian insects, and the combined phylogenetic and ecological data provide a firm foundation for further study of the position and function of these insects in ecosystems.

Current ecological studies focus on quantifying species diversity over ecosystem gradients and evaluating long-term trends in population sizes (Carson 1986; Foote and Carson, unpublished data). Among the patterns observed are changes in *Drosophila* community structure associated with invasions of nonindigenous plants and animals in Hawaii. One dominant trend is the increasing representation of the recently introduced cosmopolitan species of *Drosophila* in wet forest communities disturbed by feral pigs and alien weeds. A second pattern is the apparent decline of certain guilds of endemic picture-wing *Drosophila* and their host plants over a 20-year period of observation.

Close to one-fifth of the world's known *Drosophila* fauna are endemic to Hawaii. Invasions by nonindigenous *Drosophila* are adding to the diversity of the group. This abundance of species is increasingly useful for tracking biological diversity at several levels, from changes in chromosome inversion frequencies over altitudinal clines to the measurement of long-term changes in community structure.

Status and Trends

Methods

Beginning in 1971, as part of the International Biological Program, the relative frequencies of populations of 14 species of picture-wing *Drosophila* were measured in the Olaa Forest at Hawaii Volcanoes National Park on the island of Hawaii (Fig. 1). The fly populations were surveyed earlier by using baits placed on tree trunks, vines, and tree ferns, but the most recent survey (1992-93) used tree fern stipes exclusively. Since 1980 the surveys have employed nondestructive sampling where individuals are identified by unique wing and thorax markings in the field (Carson 1986; Foote and Carson, unpublished data).

Since 1982 four fenced feral pig exclosures have been constructed in rain forests where *Drosophila* surveys have been undertaken.

Courtesy W.P. Mull

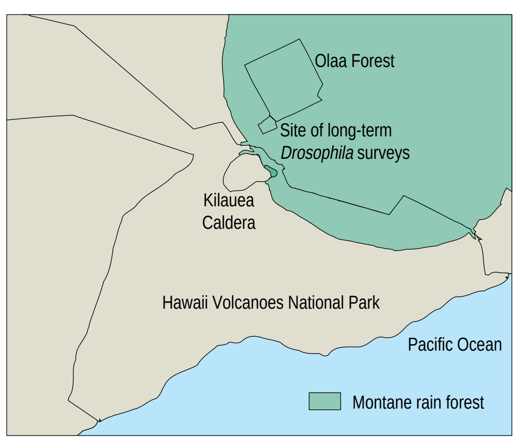
An endemic Hawaiian picture-wing *Drosophila* (*D. conspicua*-left) perched on a *Clermontia* fruit next to a cosmopolitan member of the species complex that includes *D. simulans* (right), one of the common non-indigenous species in Hawaiian rain forests. The picture-wings are close to the size of common house flies, giants in comparison to their mainland relatives.

These exclosures average about 300 ha (740 acres) in size. The impact on *Drosophila* communities of removing non-native pigs has been evaluated through the comparison of recently introduced cosmopolitan and endemic flies attracted to baits in different-aged exclosures and adjacent forest where feral pigs are still active (Foote et al., unpublished data).

Using Chromosomes To Trace Evolutionary History

There are 491 described Hawaiian species in the family Drosophilidae. Most of the species belong to one of two genera, *Drosophila* and *Scaptomyza*. Among the Hawaiian species, 124 have been genetically surveyed, including 106 of 111 picture-wing species in the genus *Drosophila* (Carson 1992). Most species are single-island endemics, reflecting the forces of geographical isolation imposed by this volcanic archipelago.

Inversion polymorphisms (*see* glossary) have been detected within or between populations of about one-third of the species and their frequencies have been measured over environmental gradients in several well-studied species on the island of Hawaii (Carson 1992). Variations in the frequency of different polymorphisms along a gradient are used as an indicator of the role of natural selection in maintaining genetic variation. One such genetic gradient occurs among populations of *Drosophila*



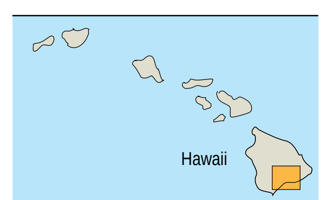


Fig. 1. Hawaii Volcanoes National Park, including the Olaa Forest, where population surveys of picture-wing *Drosophila* have been carried out.

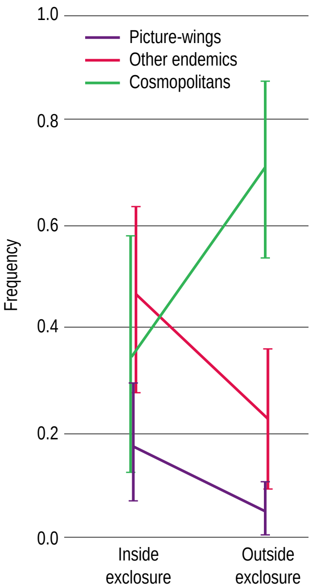


Fig. 2. A comparison of the average relative frequencies of Hawaiian picture-wing flies, other endemic *Drosophila*, and recently introduced cosmopolitan species inside and outside of a 7-year-old 240-ha (593 acre) fenced pig exclosure in Hawaii Volcanoes National Park. Frequencies are based on observations at 837 bait stations set up over five survey periods in 1992 and 1993 along four 2,400-m (7,875-ft) transects. The data are expressed as a percentage of total observations within a survey period.

silvestris above Kilauea Volcano and reflects the recolonization of habitat destroyed by two explosive eruptions within the last 2,100 years. The surfaces of Kilauea Volcano are covered by new lava flows at a rate of about 90% per 1,000 years. The population biology of Hawaiian *Drosophila* and other endemic insects has been one of continual local extinction of and recolonization by populations on single volcanoes over thousands of years (Carson et al. 1990).

Dominance of Cosmopolitan *Drosophila* in Disturbed Habitat

The dominance of non-native plant and animal species in Hawaii associated with human activity and the subsequent loss of endemic species have long been recognized (Perkins 1913). Rain forests above 1,000-m (3,280-ft) elevation provide habitat for much of the remaining native biota. Most of these wet forests occur on the "Big Island" of Hawaii where about 30% of the 500,000 ha (1.2 million acres) of upland native woodland is rain forest (Jacobi and Scott 1985). While this wet forest vegetation is among the most intact in the state, invasions by alien species have seriously degraded components of the understory.

Non-native ungulates (cattle, goats, pigs, etc.) cause major problems. Feral pigs, in particular, feed upon and uproot native tree ferns, shrubs, and herbs. They also actively consume fleshy fruits of non-native plants and thereby spread their seeds. As a consequence, feral pigs help establish non-native plants that can permanently alter native communities (Cuddihy and Stone 1990; Stone et al. 1992).

Twenty-five years ago fenced feral ungulate exclosures were first tested by Hawaii Volcanoes National Park as a method of promoting natural wet forest restoration. In the park, including approximately one-third of the Olaa Forest, exclosures encompassing as much as 800 ha (1,980 acres) are now used to manage tracts of montane wet forest (Stone et al. 1992).

When intensive research on Hawaiian *Drosophila* was initiated over 30 years ago, it was apparent that habitats altered by human activity had greatly reduced populations of endemic *Drosophila* (Carson 1967). The construction of large fenced feral pig exclosures has provided an opportunity to measure changes in *Drosophila* community composition associated with this one particular agent of disturbance in wet forests. A significant increase in the frequency of cosmopolitan species of *Drosophila* has been measured in wet forest habitat disturbed by feral pigs and associated non-native plants (Fig. 2). In areas with high pig densities, many host plants for endemic *Drosophila* are reduced to those few individuals growing as epiphytes above the reach of pigs.

In contrast, many alien plants that thrive in pig-disturbed areas are species that produce fleshy fruits eaten by the pigs. These fruit-bearing non-native plants, such as banana poka (*Passiflora mollissima*) and yellow Himalayan raspberry (*Rubus ellipticus*), also support large populations of introduced cosmopolitan *Drosophila*, such as *D. immigrans*, *D. simulans*, and *D. suzukii* (known collectively to geneticists as "yellow flies"), that breed primarily on rotting fruit (Foote et al., unpublished data).

Long-term Changes Among Populations of Picture-wing *Drosophila*

Changes in the relative proportions of different species of endemic picture-wing flies in Olaa Forest between 1971 and 1993 are shown in Fig. 3. These proportions are based upon observations of individual picture-wings, totaling 1,222 in 1971, 1,467 in 1981, and 1,294 in 1992. A general decline in overall picture-wing diversity is suggested by the observation that 4 species out of 14 were missing from one or more of the more recent surveys. There has also been a change in the relative abundances of species within the group. For example, two of the most common species of picture-wing flies from the original survey, *D. murphyi* and *D. setosimentum*, are now much less common.

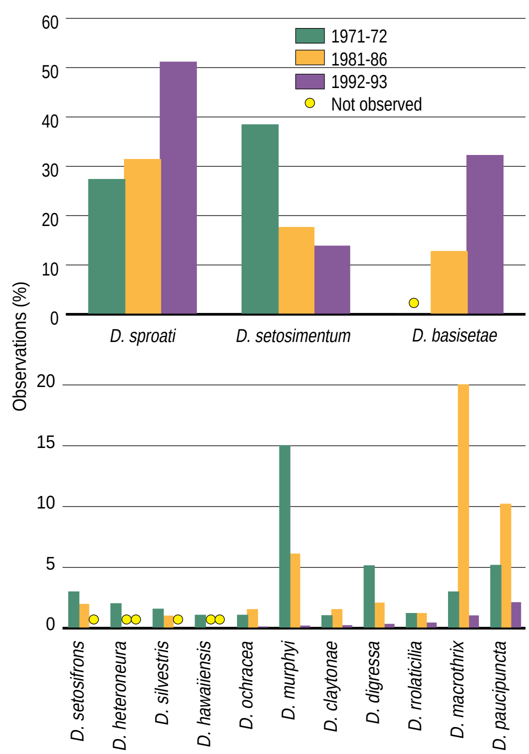


Fig. 3. A comparison of the relative frequencies of 14 endemic species of picture-wing *Drosophila* over three periods of observation from 1971 to 1993 in Olaa Rain Forest in Hawaii Volcanoes National Park. The data are expressed as a percentage of total observations within a survey period.

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Population trends are suggested by analysis of guilds of picture-wing flies that breed on specific host plants. One example is the increase in the relative frequency of observations of *D. sproati*, a species that appears to breed exclusively in rotting bark of one of the most common trees in this rain forest, the endemic member of the Aralia family, Olapa (*Cheirodendron trigynum*). In contrast, a long-term decline is evident in the guild of four species that breed primarily in rotting bark of native lobelioids in the genus *Clermontia*. There has been a concordant reduction in frequency of all four species over the last two decades and two of the four species are now missing from this site (Fig. 4).

There is historical evidence that the decline in the latter group is a consequence of the reduction of host plant populations. For example, an important host of the two picture-wings that appear locally extinct, *Clermontia hawaiiensis*, has been extirpated from at least one nearby forest with a long history of disturbance by feral pigs and cattle.

Another factor may have been the invasion of Olaa Forest by alien western yellowjackets (*Vespula pensylvanica*) in the early 1980's. The wasps have become dominant predators of other insects and may have contributed to the decline of picture-wing *Drosophila* by feeding on larvae that are particularly exposed on *Clermontia* (Carson 1986; Foote and Carson, unpublished data). These and other potential causative agents of the changes in the community structure of *Drosophila* need further investigation.

Drosophila as a Focal Taxon To Monitor Ecosystem Change

Because of the extensive data that exist on the population genetics and evolutionary relationships within the picture-wing *Drosophila*, the potential consequences of disruption of the *Drosophila* community can be examined at several levels. For instance, the loss of a local population of *Drosophila silvestris* (one of the four species that breeds in *Clermontia*) occurs at the lower end of an altitudinal cline in inversion frequencies among populations that extend above Kilauea Volcano (Carson et al. 1990). A continued decline of *D. silvestris* populations at lower elevations has the potential to change inversion frequencies. Such long-term data may prove useful in evaluating why different populations or species may not respond similarly to greenhouse stresses associated with global climate change (Hoffman and Blows 1993).

The potential influence of species extinctions of picture-wing *Drosophila* on specific lineages of subgroups (Fig. 2) can also be evaluated. For example, the guild of lobelioid-associated picture-wing flies undergoing a decline in Olaa Forest is made up of species from three separate lineages of Hawaiian *Drosophila*. Among fossil records of Hawaiian birds, an analogous situation may have occurred with the extinction of several groups of flightless geese and geeselike terrestrial herbivores (Olson and James 1991). The monitoring of focal groups of Hawaiian insects may well complement our understanding gained from vertebrates on how changes in Hawaiian ecosystems selectively favor certain taxa that make up the contemporary species diversity found in the islands.

Lastly, data from active resource management programs, such as the construction of feral pig exclosures at Hawaii Volcanoes National Park, suggest that the population declines of certain Hawaiian *Drosophila* are reversible, even in the case of local extinction. Many host populations are recovering in Olaa Forest following removal of pigs, and nearby populations of many of the missing picture-wing species persist. This is a rain forest that has twice been devastated by volcanic eruptions and has recovered. We are testing an old evolutionary tradition on these islands as we encourage the recolonization of this protected habitat by its former occupants from nearby populations.

The 30 years of intensive research on Hawaiian *Drosophila* will not be readily repeated for even a small fraction of the remaining species that make up the biological diversity present in Hawaii. The fact that Hawaiian *Drosophila* flies have received so much attention is due in part to the fact that *Drosophila* are readily observed and sampled (at baits) in native forests. The sensitivity of such groups to a wide range of human impacts needs to be evaluated. Taxa, such as Hawaiian *Drosophila*, that can be monitored in a cost-effective manner and yield statistically reliable data need to be exploited as potential indicators of the impact of environmental change on the vast majority of species about which we know too little to manage intelligently.

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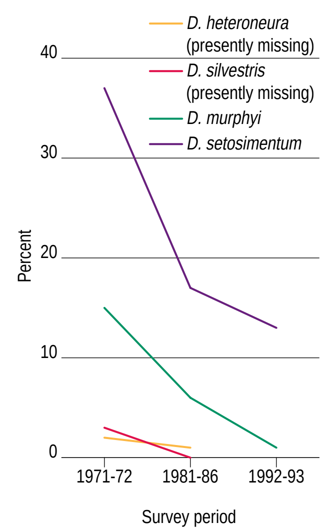

Fig. 4. Long-term trends within one host-specific guild of picture-wing *Drosophila* that breed in rotting bark of native lobelioids in the genus *Clermontia*.

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Birds of Hawaii

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The wild birds inhabiting Hawaii are unique and known worldwide. Native breeding birds rank among the world's highest in endemism, endangerment, and extinction, and Hawaii's total bird life contains a higher proportion of non-native species than perhaps any other area of comparable size. Interest in Hawaii's birds centers on the status and trends of its populations, understanding their ecological requirements, and developing measures to protect and conserve their remaining populations, which are dwindling at an alarming rate.

The unique nature of Hawaii's bird life results primarily from isolation. The Hawaiian Islands, a linear archipelago extending some 2,650 km (1,646 mi) from Kure to Hawaii, is 4,000 km (2,484 mi) from the nearest point in North America and 3,400 km (2,111 mi) from Asia. The wild colonizers, individual birds or small groups out over the ocean, were the first to stumble on Hawaii, where they remained to live and breed. This process has been going on for millions of years, with two species repeating the same process within the past 15 years. Then came evolution of new species in situ, as many of these original colonizers changed through adaptation and filled unused ecological niches in these young islands. During the past 2,000 years, humans began inhabiting the islands, bringing with them some birds that otherwise would never have reached Hawaii on their own. In addition, some strong-flying species that regularly migrate long distances have found Hawaii and developed annual migration patterns that bring them to the islands for part of each year during the nonbreeding season.

Current Status

It is convenient to categorize the wild birds of Hawaii into residents and visitors. Resident species remain permanently in Hawaii; visitors regularly come to Hawaii for only part of each year. Each group can be further divided. Residents are either native species that arrived or evolved here naturally or alien species brought in by humans. Visiting birds either come to Hawaii to breed or breed elsewhere and come during nonbreeding season. True pelagic species, which spend all their time at sea except when breeding, are considered to have visited Hawaii if they have occurred in Hawaii's offshore waters within the 200-nautical mile zone.

Native Residents

Native resident species may be either indigenous, meaning that others of the same species or subspecies reside elsewhere in the world, or endemic, meaning that they are found nowhere else. The latter may be endemic at subspecies level, at species level, or at genus or higher level. For example, endemic at subspecies level means that others of its species are found elsewhere, but the subspecies occurs only in Hawaii.

Alien Residents

Polynesians first settled in Hawaii roughly 2,000 years ago (Kirch 1982). Only one bird species brought by the early Polynesians still survives in Hawaii as an established alien species, the red junglefowl (*Gallus gallus*), ancestor of the domestic chickens. The

Hawaiians called it *moa*, not to be confused with the huge, extinct, flightless birds in New Zealand of the same name. How many other bird species may have been brought by the Polynesians and failed to become established is unknown.

Since Captain Cook first visited Hawaii in 1778, alien bird species have been brought to the islands in a steady stream. Only a few have been successful in establishing a continuing breeding population. Of the 54 alien species now considered to have established populations, fully half have origins in Asia (Fig. 1). Fewer are from North America and Africa; a few have come from Australia and South America. Among the continents, only Antarctica is not represented by an established alien species. Penguins have indeed been brought to Hawaii, and one thriving population is in captivity today. But were they to escape, they would not find sufficient krill and ice to maintain a wild population in the islands.

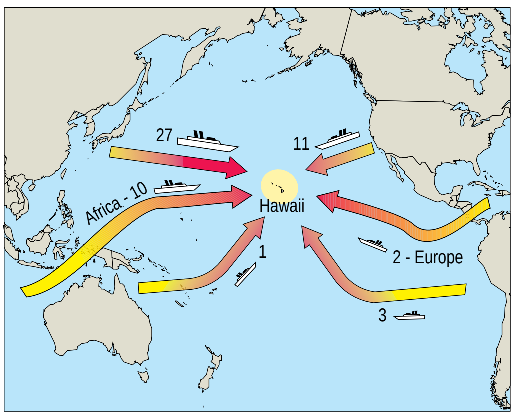

Fig. 1. Origins of the 54 alien species established in Hawaii.

Breeding Visitor Species

Visiting species that come to Hawaii to breed are basically pelagic, that is, living on the open ocean. They come to land to breed, but depart again as soon as parental duties end. Many go to the food-rich boundaries of ocean currents just north of the equator, but some species range throughout the North Pacific (Fig. 2). None appears at any other land during nonbreeding season. First-year birds of most species remain at sea for 3 years or more before returning to breed. Breeding visitors are the albatrosses, shearwaters, petrels, terns, and some tropicbirds. Other seabird species, including boobies, frigatebirds, and noddies, are classed as residents since they remain based at their breeding areas throughout the year, going to sea usually for only a few days at a time.

Nonbreeding Visitor Species

A great many birds that breed elsewhere

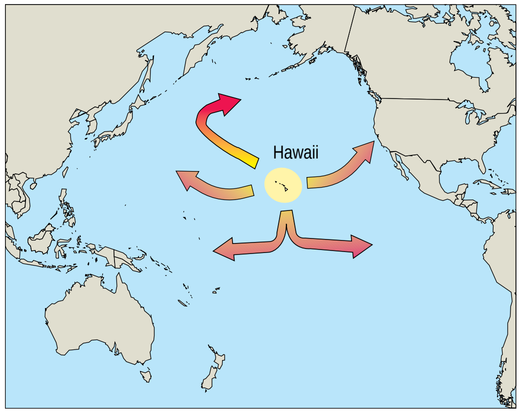

Fig. 2. Dispersal of the 13 breeding visitor species when not breeding.

depart their nesting grounds after chick rearing is finished, some wandering freely and others following traditional migration routes. Some species, notably the familiar Pacific golden-plover (*Pluvialis fulva*) and some other shorebirds and ducks, have developed migration patterns that bring large numbers to Hawaii regularly each year, with some individuals even coming to the same plot of ground each winter (Johnson et al. 1981). For other species, just a few individuals turn up each year. For still others, an individual or two may be reported in only a few years out of ten. A number of species have been recorded in Hawaii fewer than a dozen times, perhaps only once or twice. All regular visitors and most others are strong flyers, accustomed to making long migration flights annually, or are larger birds able to store enough energy to reach Hawaii on their own. Almost all are waterbirds. Only nine species of passerine landbirds are known to have straggled to Hawaii, and most of these have been recorded only one or two times each. *Note that absolutely no species of small landbird migrates regularly to Hawaii, either for breeding or in nonbreeding season*. Virtually all nonbreeding visitor species nest in the northern hemisphere, most of them in the far north (Fig. 3). A few shearwaters and petrels, a skua, and the great crested tern (*Sterna bergii*) are the only exclusively southern hemisphere nesters that have straggled to Hawaii.

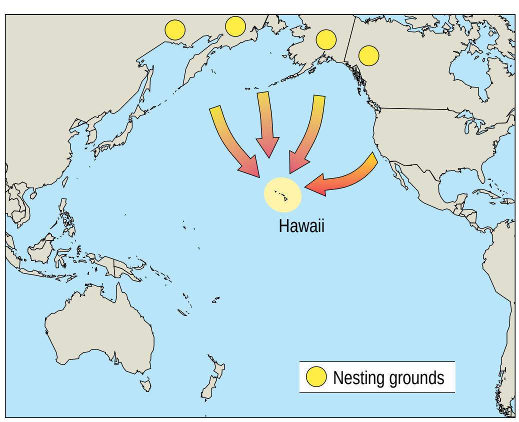

Fig. 3. Origins of the 155 visitor species that do not breed in Hawaii.

All Species

Of the 272 species resident now or recorded as visitors (Pyle 1992), roughly 40% are permanent residents, about equally divided between native and alien species (Fig. 4). The breeding visitors, all seabirds, are relatively few. The remaining 55% of the species are nonbreeding visitors. This large percentage for nonbreeding visitor species is not surprising, since these include many species that have wandered to Hawaii as individual stragglers. But in terms of total individuals, the picture is reversed. The nonbreeding visitor species account for probably the fewest individuals, while the breeding visitor seabirds have much larger populations in their huge nesting colonies in the unpopulated Northwest Hawaiian Islands. But the largest of all in total population are the alien residents, which include the ubiquitous Japanese white-eye (*Zosterops japonicus*), zebra dove (*Geopelia striata*), and other residents found almost everywhere in the main populated islands.

Birds known to have been in Hawaii in the past, but which are no longer there, can be summarized as follows: 16 species (resident-native) have become extinct since Captain Cook's visit; 35 or more species (subfossils, probably native residents) were extinct before Captain Cook's visit; and about 150 species are alien introductions not established. Adding these to the 272 species here now constitutes about 475 species of birds known to have occurred in Hawaii.

Trends

Native Landbirds

Meaningful estimates of total populations of landbirds in Hawaii are difficult to derive. Native species have been confined, at least since Captain Cook's visit, to thickly vegetated and wet higher elevation forests on steep slopes or occupied by deep muddy bogs. Not surprisingly, naturalists over the years could make no real estimates of landbird populations for the island group or even for an individual island, despite the relatively small total areas that were occupied by many of these endemic species.

It was not until the Hawaii Forest Bird Survey in the late 1970's to early 1980's that thoroughly planned fieldwork was conducted, leading to the first comprehensive population estimates for native Hawaiian landbirds. Pioneering techniques for field surveys in such terrain and for statistical analysis were used to obtain population estimates for the native landbird species on all forested islands except O'ahu and Ni'ihau (Scott et al. 1986, 1988). For O'ahu Island, Shallenberger's surveys during the latter 1970's in the Koolau Mountains (Shallenberger and Vaughn 1978) and in the Waianae Mountains (unpublished) have been the most comprehensive.

More recently, Ellis et al. (1993) estimated populations for each native forestbird on each Hawaiian island, based on information available at the end of 1992. These are not directly comparable with the earlier estimates derived from field surveys. However, these estimates and numerous other less comprehensive surveys over the years involving some species on some islands do reinforce a general consensus that Hawaiian forestbirds have declined steadily both in the long term during the past century and in the short term in the past decade.

Resident Waterbirds and Visitors

The Hawaii Division of Forestry and Wildlife has conducted statewide counts of wetland birds semiannually during recent decades. These have included resident wetland species (not the seabirds) and nonbreeding visitor species. Variations in these population counts over the years reflect changes in available wetland habitat, thoroughness of coverage, and possibly some irregular interisland movements. Engilis and Pratt (1993) analyzed these statewide counts for the resident species during 1978-87. Data from earlier surveys covering only certain islands and using less rigorous counting techniques are not readily comparable. Longer-term historical trends in populations of four endangered wetland species are being examined for the Hawaii Wetland Bird Recovery Plan now in preparation by the Recovery Team for the U.S. Fish and Wildlife Service (A. Engilis, personal communication).

The breeding visitor seabirds gather to nest in large colonies in the Northwest Hawaiian Islands. Gross estimates of population numbers for these species made in the 1960's and again in the late 1970's are not comparable for trends analysis because of varying techniques used in attempting to arrive at meaningful numbers in these huge colonies totaling in the millions. Harrison (1990) discussed the difficulties involved in making representative counts and finds no evidence of long-term trends in species numbers, although some wide fluctuations occurred earlier this century. One notable feature has been the return of the Laysan albatross (*Diomedea immutabilis*) as a breeding visitor to Kaua'i and O'ahu in the main Hawaiian Islands. Since 1977, a steady increase in numbers now measured in the hundreds has local interest but has had a rather small effect on the total statewide population of millions.

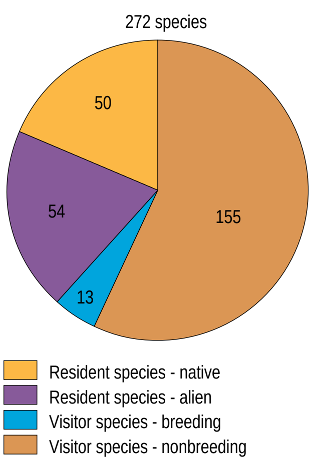

Fig. 4. Bird species currently resident in or visiting Hawaii.

Extinction

The rate of extinction within Hawaii's endemic birds is by far the highest in the United States and is approached worldwide only within a few other isolated island groups. At the time of Captain Cook's visit in 1778 some 93 species and subspecies of native birds were breeding in Hawaii, as determined by subsequent discovery and scientific description. In the ensuing two centuries, at least 23 of these have gone extinct (A.O.U. 1983) and another 13 are imperiled. Recent discoveries of the bones of prehistorically vanished species now reveal a vast array of former birds that became extinct long before Captain Cook arrived. Thirty-five of these have already been scientifically described (Olson and James 1991) and must represent only a small fraction of the forms of birds that existed prehistorically in Hawaii.

Extinctions over the past 200 years (Fig. 5) show a disproportionate number of bird species vanishing during the 1890's, a decade concluding a period of intense discovery and collecting of Hawaii's birds. A similar large decline in the 1980's represents nine forms not reported since then. Ralph and van Riper (1985) discussed the factors that have contributed to the decline in Hawaiian bird populations since the arrival of the Polynesians.

Aliens

An early listing of the alien species in Hawaii was that of Caum (1933), who identified 92 species as alien introductions. These may be categorized as established, not established, or uncertain. Most (75%) of the alien species established in 1933 are still present (Pyle 1992). Few of those deemed uncertain or not established in 1933 have persisted until today. Introductions continued during the 1940's and 1950's but thereafter were severely curtailed by stronger governmental restrictions on importation of wild birds. Of the 54 alien species considered established in Hawaii today, 31 (57%) had been introduced more than 60 years ago, and 23 (43%) have been introduced and have become established since 1933.

Conclusion

Hawaii's birds comprise four groups: native and alien resident species, and breeding and nonbreeding visitor species. Factors affecting population levels differ markedly among the groups. Although current status of species within all groups is fairly well understood, assessing meaningful trends for species is difficult for lack of comparable quantitative data on statewide populations over time.

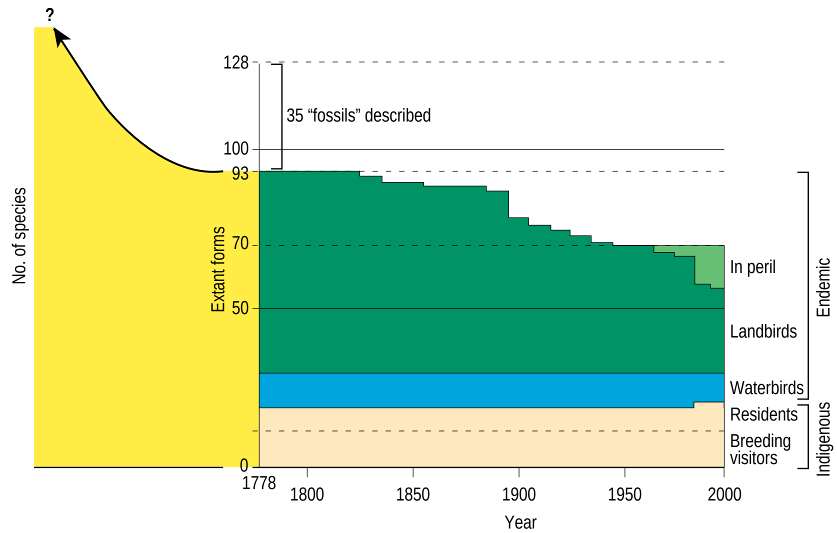

Fig. 5. Extinction of native breeding birds since 1778. Steps mark the decade of the last record for each form considered extinct (A.O.U. 1983). The 70 forms shown as currently existing include 13 in peril, with steps marking the decades of their last known records. Yellow represents prehistoric forms.

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Hawaii's Endemic Birds

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The endemic landbirds of Hawaii, particularly the Hawaiian honeycreepers, an endemic subfamily of the cardueline finches, are one of the world's most dramatic examples of adaptive radiation and speciation (*see* glossary) in island ecosystems (Freed et al. 1987; Scott et al. 1988). From what is believed to have been a single successful colonization of the Hawaiian Archipelago by an ancestral species from North America, the honeycreepers evolved into a diverse array of species and subspecies of birds with bills ranging from thick, seed-eating beaks of the palila (*Loxioides bailleui*), to small insectivorous bills as seen on the `amakihi (*Hemignathus virens*), woodpecker-like adaptations of the `akiapola`au (*H. munroi*), and large, decurved nectar-feeding bills of the `i`iwi (*Vestiaria coccinea*).

In addition to the honeycreepers, the historically documented endemic Hawaiian avifauna included three seabirds, several waterfowl, two raptors, and perching birds that include a species of crow, and representatives of Old World flycatchers, honeyeaters, and thrushes. In all, at least 71 endemic species and subspecies of Hawaiian birds existed at the time of Captain Cook's arrival in the Hawaiian Islands in 1778. Now, however, 76% of the Hawaiian birds are either extinct or endangered, and several of the remaining unlisted species are showing significant population declines.

The arrival of humans to the Hawaiian Islands—starting with the Polynesians more than 1,500 years ago and continuing following European contact—drastically changed many natural ecosystems, leading not only to the extinction of many plant and animal species, but also to a significant reduction in both range and abundance for many other taxa. Originally, the Hawaiian birds were found in all habitat zones on each island, but today few native forest birds are found below 610-m (2,000-ft) elevation, and many of the wetland areas that once provided abundant habitat for waterbirds have been destroyed.

Of the historically documented 71 taxa of endemic Hawaiian birds, 23 are now extinct, and 30 of the remaining 48 species and subspecies are listed as endangered or threatened by the U.S. Fish and Wildlife Service (USFWS 1992), many with few or only single populations remaining (Fig. 1; Table 1; Table 2). Studies of recently discovered fossil bird bones have further identified nearly 40 additional species of Hawaiian birds never seen alive by the post-Cook naturalists; many of these became extinct after the Polynesians arrived (Olson and James 1982; H. James, Smithsonian Institution, personal communication).

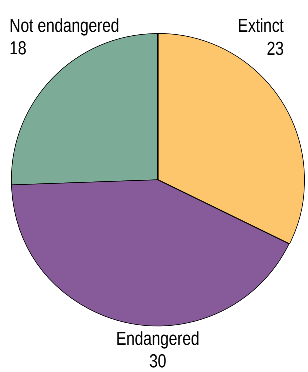

Fig. 1. Current status of endemic Hawaiian bird species known to exist at the time of Western contact (1778).

Table 1. Historically known endemic Hawaiian birds that are now extinct.

Common name	Scientific name	Island distributions
Hawaiian rail	*Porzana sandwichensis*	Hawaii
Laysan rail	*P. palmeri*	Laysan
Laysan millerbird	*Arcrocephalus f. familiaris*	Laysan
`Amaui	*Myadestes oahuensis*	Oahu
Oloma`o	*M. l. lanaiensis*	Lanai
Oahu `o`o	*Moho apicalis*	Oahu
Hawaii `o`o	*M. nobilis*	Hawaii
Kioea	*Chaetoptila angustipluma*	Hawaii
Lanai hookbill	*Dysmorodrepanis munroi*	Lanai
Lesser koa-finch	*Rhodacanthis flaviceps*	Hawaii
Greater koa-finch	*R. palmeri*	Hawaii
Kona grosbeak	*Chloridops kona*	Hawaii
Greater `amakihi	*Hemignathus sagittirostris*	Hawaii
Oahu `akialoa	*H. obscurus ellisianus*	Oahu
Lanai `akialoa	*H.o. lanaiensis*	Lanai
Hawaii `akialoa	*H.o. obscurus*	Hawaii
Oahu nukupu`u	*H.l. lucidus*	Oahu
Lanai creeper	*Paroreomyza m. montana*	Lanai
Oahu `akepa	*Loxops c. rufus*	Oahu
`Ula-`ai-hawane	*Ciridops anna*	Hawaii
Hawaii mamo	*Drepanis pacifica*	Hawaii
Black mamo	*D. funerea*	Molokai
Laysan honeycreeper	*Himatione sanguinea freethii*	Laysan
Total number extinct		23

Reasons for the Decline

Many factors have been suggested to explain the decline of Hawaiian bird species since human colonization (Ralph and van Riper 1985; Scott et al. 1988). The most important and plausible of these include habitat loss (Berger 1981; Kirch 1982; Olson and James 1982; Jacobi and Scott 1985), susceptibility to introduced avian diseases (Warner 1968; Ralph and van Riper 1985; van Riper et al. 1986), predation by introduced mammals (Atkinson 1977), and competition from introduced birds (Mountainspring and Scott 1985) and arthropods (Perkins 1903; Banko and Banko 1976). Although no one factor is believed to be the single cause for the loss or decline of the Hawaiian birds, many biologists believe that habitat loss and avian diseases have had the greatest effect on native birds.

Habitat Loss

Habitat loss from forest removal and development in the Hawaiian Islands started when large tracts of mostly lower elevation land were cleared for agriculture by the first Hawaiian colonists. After European and American settlers arrived, starting in the late 18th century, habitat loss increased dramatically as agriculture and ranching expanded. Today, less than 40% of the land surface of Hawaii is covered with native-dominated vegetation (Jacobi 1990; S. Gon, The Nature Conservancy of Hawaii, unpublished data). Some of the most significant loss of habitat has occurred below 610 m (2,000 ft)

Table 2. Status of extant species and subspecies of endemic Hawaiian birds. Data summarized from Scott et al. (1986), Harrison (1990), Ellis et al. (1992), Engilis and Pratt (1993), and J. Jacobi (unpublished data).

Species	Island distributions[a]	Listing status[b]	Estimated population	Population data source[c]	No. of populations	Trend[d]	Comments
Dark-rumped petrel *Pterodroma phaeopygia sandwichensis*	All?	E	400-600	2	5 ?	Unk	Upland nester; stable on Ma with predator control
Newell's shearwater *Puffinus newelii*	All?	T	4,000-6,000	2	4 ?	Unk	Upland nester; susceptible to predators
Nene (Hawaiian goose) *Branta sandvicensis*	Ka,Ma,Ha	E	< 500	3, 5	4	S ?	Recently introduced population on Ka increasing
Koloa (Hawaiian duck) *Anas wyvilliana*	Ka,Oa,Ha (Ma, Mo)	E	2,500	4	3	S ?	Problem of hybridization with mallards on Oa
Laysan duck *A. laysanensis*	NW	E	< 50	3	1	D	Population declined from > 600 to < 50 since 1990
Hawaiian hawk *Buteo solitarius*	Ha	E	1,500-2,500	3, 5	1	S	Occupies native and non-native forest
Hawaiian moorhen *Gallinula chlorpus sandwicensis*	Ka,Oa (Mo,Ma,Ha)	E	Unk	4	2	Unk	Difficult species to survey; no reliable population count data
Hawaiian coot *Fulica americana alai*	All	E	2,000-4,000	4	5	S ?	Population fluctuations may result from addition of migrating birds
Hawaiian stilt *Himantopus mexicanus knudseni*	All	E	1,200-1,600	4	6	I ?	Increase on Oa and Ma due to habitat managment
Hawaiian noddy *Anous minutus melanogenys*	All		Many thousands	2	?	S ?	Frequent along ocean cliffs of all islands
Pueo (Hawaiian owl) *Asio flammeus sandwichensis*	All	C	3,500 ?	3	7	D ?	No detailed data on population trends
`Alala (Hawaiian crow) *Corvus hawaiiensis*	Ha	E	< 20	5	1	D	An additional 18 birds in captivity
Nihoa millerbird *Acrocephalus familiaris kingi*	NW	E	< 300	3	1	S	Extremely vulnerable; entire population on one island
Kauai `elepaio *Chasiempis sandwichensis sclateri*	Ka		> 20,000	1, 5	1	D ?	Relatively common in suitable habitat
Oahu `elepaio *C.s. gayi*	Oa	C	200 ?	5	2	D	Few birds seen in recent years
Hawaii `elepaio *C.s. sandwichensis*	Ha		> 200,000	1, 5	3	S ?	Widespread, even in mid-elevations
Kama`o *Myadestes myadestinus*	Ka	E	< 50 ?	1, 5	1	EX ?	Not seen in over 5 years; possibly extinct
Oloma`o *M. lanaiensis rutha*	Mo	E	< 10 ?	1, 5	1	EX ?	Not seen in over 5 years; possibly extinct
`Oma`o *M. obscurus*	Ha		>170,000	1, 5	1	S	Extinct from Kona and Kohala sections of island
Puaiohi *M. palmeri*	Ka	E	< 50 ?	1, 5	1	D	Extremely rare; seen in 1994 survey
Bishop's `o`o *Moho bishopi*	Ma (Mo)	EX?	?	1, 5	?	EX ?	Extinct? No recent black bird populations
Kauai `o`o *M. braccatus*	Ka	E	< 10 ?	1, 5	1	EX ?	Not seen since 1986
Laysan finch *Telespyza cantans*	NW	E	10,000	3	1	S	Translocated population on Perl and Hermes Reef
Nihoa finch *T. ultima*	NW	E	1,000-3,000	3	1	S	Extremely vulnerable; entire population on one island
`O`u *Psittirostra psittacea*	All (Oa,Mo,La Ma)	E	< 50 ?	1, 5	2	D, EX ?	Rapid decline on Ka and Ha; last seen in 1986 on Ha
Palila *Loxioides bailleui*	Ha	E	> 3,000	1, 5	1	S ?	Habitat extremely vulnerable to fire
Maui parrotbill *Pseudonestor xanthophrys*	Ma	E	< 500	1, 5	1	D	Recent decline in distribution
Kauai `amakihi *Hemignathus virens stejnegeri*	Ka		> 15,000	1, 5	1	S ?	Population seems stable
Oahu `amakihi *H.v. chloris*	Oa		20,000-60,000	5	2	S	Also in areas with non-native vegetation
Maui `amakihi *H.v. wilsoni*	Ma,Mo (La)		> 45,000	1, 5	4	S	Last seen on La in 1970's
Hawaii `amakihi *H.v. virens*	Ha		> 800,000	1, 5	Many	S	Population seems stable
`Anianiau *H. parvus*	Ka		15,000-25,000	1, 5	1	S	Common in suitable habitat
Kauai `akialoa *H. procerus*	Ka	E	< 10 ?	1, 5	1	D, EX ?	Not seen in 30 years
Kauai nukupu`u *H. lucidus hanapepe*	Ka	E	< 10 ?	1, 5	1	D, EX ?	Last seen in 1986
Maui nukupu`u *H.l. affinus*	Ma	E	< 10 ?	1, 5	1	D, EX ?	Not seen in nearly 10 years
`Akiapola`au *H. munroi*	Ha	E	< 1,500	1, 5	4	D	Nearly extinct on upper slopes of Mauna Kea

—continued—

Table 2. Continued.

Species	Island distributions[a]	Listing status[b]	Estimated population	Population data source[c]	No. of populations	Trend[d]	Comments
Kauai creeper *Oreomystis bairdi*	Ka	C	800-1,000	1, 5	1	D	Population now concentrated in central Alakai region
Hawaii creeper *O. mana*	Ha	E	12,500	1, 5	3	S ?	Uncommon but appears stable
Oahu creeper *Paroreomyza maculata*	Oa	E	< 10 ?	5	1	D, EX ?	Last seen in 1985
Molokai creeper *P. flammea*	Mo	E	< 10 ?	1, 5	1	D, EX ?	Not seen since the 1960's
Maui creeper *P. montana newtoni*	Ma		35,000	1, 5	2	S	Common in wet and mesic forests >1,220-m elevation
Kauai `akepa *Loxops coccineus caeruleirostris*	Ka	C	> 3,000	1, 5	1	D	Population has been declining over past 10 years
Maui `akepa *L.c. ochraceus*	Ma	E	< 10 ?	1, 5	1	D, EX ?	Not seen during past 10 years
Hawaii `akepa *L.c. coccineus*	Ha	E	14,000	1, 5	3	D ?	Locally common in upper-elevation forests
`I`iwi *Vestiaria coccinea*	All		> 350,000	1, 5	7	S/D	Appears stable on Ka, Ma, and Ha; rare or EX elsewhere
`Akohokohe *Palmaria dolei*	Ma (Mo)	E	>3,500	1, 5	1	S ?	Locally common above 1,220 m; EX on Molokai
`Apapane *Himatione s. sanguinea*	All		> 1,300,000	1, 5	7	S	Very common above 1,220 m, less common below
Po`o-uli *Melamprosops phaeosoma*	Ma	E	< 50	1, 5	1	D	Last seen in 1993; extremely rare
Total number of extant species	48						

[a]Islands: All — all major Hawaiian Islands; Ha — Hawaii; Ka — Kauai; La — Lanai; Ma — Maui; Mo — Molokai; NW — Northwest Hawaiian Islands; Oa — Oahu; species extinct where island listed in parentheses.
[b]Listing status: C — candidate for listing; E — endangered; EX — extinct; T — threatened species.
[c]Population and trend data source: 1 — Scott et al. (1986); 2 — Harrison (1990); 3 — Ellis et al. (1992); 4 — Engilis and Pratt (1993); 5 —recent survey data (J. Jacobi, unpublished data).
[d]Trend: D — declining; EX? — possibly extinct; I — increasing; S — stable; Unk — unknown.

elevation, where less than 10% of the native vegetation remains. In addition to direct clearing, all remaining native plant communities are further degraded by disturbance and competition from introduced plants and animals.

The current ranges of most Hawaiian forest birds appear closely tied to the distribution of forests dominated by native tree species. It is unclear whether this association is due to feeding specialization on native plants, or if other factors, such as disease or predators, restrict native birds from disturbed habitats. The only real exception to this is the Oahu `amakihi (*Hemignathus virens chloris*), which recently appears to be colonizing habitats dominated by introduced plant species around Honolulu.

Avian Disease

The accidental introduction of *Culex* mosquitoes in the early 19th century, and the importation and widespread release of domestic fowl, gamebirds, and cage birds with their accompanying diseases, are believed responsible for the establishment of avian pox virus and malaria (*Plasmodium relictum*) in Hawaiian forest bird populations (Warner 1968; van Riper et al. 1986). The concurrent fragmentation of native forests probably hastened the spread of mosquitoes and exotic birds into forest habitats, exposing native birds to avian pox (Perkins 1893; Henshaw 1902) and malaria.

Warner (1968) first identified pox and malaria as major pathogens of native forest birds. Van Riper et al. (1986) demonstrated that the highest incidence of malaria occurs in wet midelevation forests (between 900 m [3,000 ft] and 1,500 m [5,000 ft]) where populations of *Culex* mosquitoes overlap with highly susceptible native birds. Current investigations support these observations. Surveys for other disease agents identified a number of potentially pathogenic parasites and bacteria, but none has been implicated as a significant cause of mortality (van Riper and van Riper 1985).

Introduced Predators

While introduced rats (*Rattus* spp.), cats (*Felis catus*), dogs (*Canis familiaris*), and mongooses (*Herpestes auropunctatus*) have seriously affected nesting waterbirds, less information exists on the significance of these predators in restricting the distribution and abundance of upland forest birds in Hawaii (Atkinson 1977; Griffin et al. 1989). Several projects have begun in Hawaii to develop adequate control strategies for introduced predators and to monitor the response of forest bird populations to the reduction or elimination of these predators.

Competition and Food

Competition for nesting and food resources by introduced birds and food resource limitation by introduced arthropods (e.g., ants or wasps) are the two most difficult of the limiting factors hypotheses to evaluate. Although a study by Mountainspring and Scott (1985) found a negative association between several native and introduced bird species pairs, much more work is needed to understand the significance of these relationships. Similarly, preliminary evidence suggests that arthropods such as the introduced yellowjacket wasps (*Vespula* spp.) and several species of ants may seriously deplete the resident arthropods that many native birds eat, particularly during nesting (P. Banko, NBS, personal communication).

Current Status

Table 2 summarizes the most recent information on the status of endemic Hawaiian bird species. The population size for many forest birds comes from the Hawaii Forest Bird Survey, 1976-81 (Scott et al. 1986). While most of these numbers are more than 15 years old, they represent a distribution and abundance baseline upon which subsequent surveys can be based. The trend information in Table 2 is based on population surveys conducted during the past 15 years.

Seabirds

Three seabird species are endemic to Hawaii: the endangered dark-rumped petrel (*Pterodroma phaeopygia sandwichensis*), the threatened Newell's shearwater (*Puffinus newelii*), and the Hawaiian noddy (*Anous minutus melanogenys*). The first two relatively rare species nest in upland forest or subalpine and alpine sites. As with all of the ground-dwelling or nesting birds, the dark-rumped petrel and Newell's shearwater are extremely susceptible to predation by cats, dogs, rats, and mongooses during their long nesting period. A successful predator-control program in nesting areas for the dark-rumped petrel in Haleakala National Park on Maui has resulted in a significant increase in petrel productivity. Recently discovered nesting areas for the dark-rumped petrel and Newell's shearwater on the island of Hawaii offer similar opportunities to use predator control to reestablish significant breeding colonies for these species in upland habitats.

Waterbirds

Historically, the Hawaiian avifauna includes six waterbird species, five of which are typically found in and around fresh-, brackish-, and saltwater impoundments and estuaries (Engilis and Pratt 1993). The sixth species, the nene or Hawaiian goose (*Branta sandwichensis*), though occasionally found around water, most typically occurs in upland sites.

Continued loss of habitat and predation are the two biggest threats to the remaining Hawaiian waterbirds. Although the Hawaiian coastal zone formerly contained many large wetland areas, few remain. For example, the resort area known as Waikiki Beach was an extensive wetland that was drained in the early 1900's. Because introduced predators are a major threat to waterbirds in Hawaii, predator control has become essential in all waterbird-management programs.

An intensive captive propagation and release program has kept the nene from extinction. This ground-nesting goose, however, is extremely vulnerable to predation by introduced mongooses, cats, dogs, and possibly rats and is not able to sustain wild populations in most areas (Stone et al. 1983). A recently established population on the island of Kauai appears to be thriving, probably mostly because of the absence of mongooses on this island.

Both duck species endemic to Hawaii are endangered. The Laysan duck (*Anas laysanensis*) is known only from Laysan Island, a small atoll about halfway up the northwest Hawaiian Island chain. Although population levels have been as high as 600 birds over the past 25 years, they dropped to fewer than 50 during 1993 (T. Work, NBS, personal communication). Species confined to such a small geographical area are extremely vulnerable to natural disasters (e.g., hurricane damage) or human-related impacts (e.g., introduction of disease or predators to the island).

The koloa or Hawaiian duck (*A. wyvilliana*), formerly found on all major Hawaiian Islands, is now relatively rare, with small populations on Kauai, Oahu, and Hawaii. It, too, is extremely vulnerable to predators. Additionally, because koloa on Oahu are hybridizing with feral populations of the closely related mallard (*A. platyrhynchos*; Engilis and Pratt 1993), a mallard-control program has been recommended to protect the native koloa populations from genetic alteration.

Courtesy J. Jeffrey Photography©

`I`iwi (*Vestiaria coccinea*). The long sickle-bill of the `i`iwi enables it to feed on nectar from flowers and to probe for insects.

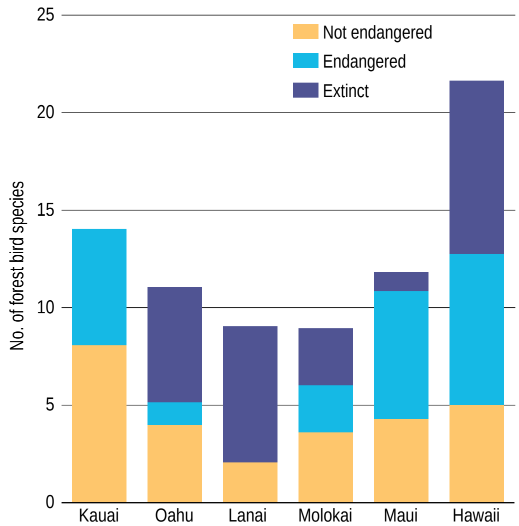

Fig. 2. Summary of status of endemic forest birds on the major Hawaiian Islands.

In addition to the waterbirds, the two rail species endemic to Hawaii are now extinct. One species, the Laysan rail (*Porzana palmeri*), known only from Laysan Island, became extinct after introduced rabbits nearly totally defoliated this small atoll in the early 1900's (Berger 1981). The other rail species endemic to Hawaii (*P. sandwichensis*) was extremely rare in the late 1700's when Western naturalists first began to document the Hawaiian birds. This species was probably extinct by the early 1900's (Berger 1981).

Forest Birds

Forest birds constitute the largest group of Hawaiian birds, with 60 species and subspecies described since Western contact. Several species of passerines known from the Northwest Hawaiian Islands are also included with the forest bird group, although none of these atolls has any forest habitat.

Both the greatest number of species and the number of losses of species of Hawaiian birds are found in the forest bird group. Of 60 endemic species and subspecies of Hawaiian forest birds, 22 are believed extinct, an additional 23 are endangered or threatened (USFWS 1992), and 4 are candidate species for listing (Table 2). Thirteen of the endangered forest birds have estimated populations of less than 50 individuals; 10 of these species have not been sighted during the past 10 years and may be extinct. The island of Kauai, which seemed to be the only island with all historically known bird species still extant, now has five species that may be extinct (Fig. 2). Surveys in 1993 and 1994 resulted in finding only one of the endangered forest bird species, the puaiohi or small Kauai thrush (*Myadestes palmeri*).

Only 11 Hawaiian forest bird taxa are considered relatively stable, but several populations of these species, particularly the \`i\`iwi, have experienced recent declines. The \`oma\`o or Hawaii thrush (*M. obscurus*) has relatively robust populations on the windward side of the island of Hawaii, but is extirpated in the wet forests of both the leeward (Kona) side of the island and in the Kohala region.

Conservation Outlook

While the prospects for survival of all remaining Hawaiian bird species appear limited, conservation efforts to further the chances of survival of even some of the rarest species can be enhanced by using techniques such as translocation, predator and disease vector control, and captive propagation in conjunction with habitat-management programs.

Avian Disease Research and Management

Since 1992 the National Biological Service's disease studies have focused on determining the effect of pox and malaria transmission on the island of Hawaii and whether significant changes in the prevalence and distribution of these diseases have occurred since van Riper and colleagues completed their work in the late 1970's. Major new efforts to develop strategies for monitoring transmission of these diseases in remote forest habitats and for controlling vector populations are in progress.

In 1992 NBS scientists witnessed a major pox and malaria epidemic in midelevation forest birds on the island of Hawaii. These birds are highly susceptible to malaria. Results of experimental infections with isolates of malaria from wild birds demonstrated that a minimal infective dose, equivalent to the bite of a single malaria-infected mosquito, was sufficient to kill 90% of juvenile \`i\`iwi under experimental conditions. The high susceptibility of this species could explain its disappearance during the past 20 years from many midelevation forests where it was previously common.

Strategies for breaking the cycle of vector-transmitted diseases include intensive environmental management to reduce mosquito breeding sites, chemical and biological control agents, genetic manipulation of the vector population, and release of sterile male mosquitoes. In addition, removal of feral ungulates from critical forest habitats may reduce available breeding sites and mosquito densities to levels too low to support disease transmission, but this needs to be evaluated under controlled conditions. Efforts by land managers in Hawaii to fence and control feral ungulates will provide an opportunity to coordinate disease research with management.

Additional Research and Management

Conservation programs in Hawaii need to have both species and ecosystem components.

Species actions include intensive site-management programs (e.g., predator control, disease and vector control, food supplementation, detailed ecological research, nest manipulation), coupled with translocation and state-of-the-art captive propagation and reintroduction. These strategies are being applied to the critically endangered `alala or Hawaiian crow (*Corvus hawaiiensis*). During 1993 the remaining wild population of 12 `alala was augmented with the release of 5 juvenile birds hatched in captivity from eggs removed from wild nests. Limited nesting success in the remaining three wild pairs prompted a "double-clutching" (*see* glossary) strategy to increase egg productivity and allow for artificial incubation and hatching. Two other birds hatched from artificial incubation of wild-laid eggs were added to a captive breeding flock; the 1994 season yielded five chicks from wild nests and four new birds from captive breeding.

Habitat and ecosystem management are also essential to conserve the remaining Hawaiian birds, as well as for recovery of rare and listed species. Unless we can better protect the natural ecosystems in Hawaii today, the already enormous list of endangered and extinct species known from the Hawaiian Islands will grow and species that are still common will also decline.

Courtesy J. Jeffrey Photography©

Palila (*Loxioides bailleui*) perched in a mamane (*Sophora chrysophylla*) tree. This endemic forest bird feeds primarily on the immature seeds of the mamane.

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